Eclosion and Duration of Larval Development in the Alkali Bee, *Nomia melanderi* Cockerell[1]

(Hymenoptera : Apoidea)

G. A. HACKWELL[2] AND W. P. STEPHEN
Oregon State University, Corvallis

There are few detailed studies available on the larval development in clistogasterous Hymenoptera in general and in the bees in particular. The secluded habitats in which the immatures of these insects develop are environmentally so stable that their exposure for purposes of observation usually results in the loss of the specimens.

Published accounts generally accede to the presence of five larval instars in the honey bee, *Apis mellifera* L., and they credit the original data to Bertholf (1925). However, nowhere in the latter paper does the author state unequivocally that five instars exist, and his tabular data lack clarity on this point. Apparently, there is not complete accord on this point, for Bier (*in* Büdel-Herold, 1960) claims that there are six molts from the egg to the adult honey bee; that is, four larval molts, one to the pupa and the last to the adult. Among other bees, the number of larval instars is reported to be three or four. Cross and Bohart (1960) report that unpublished measurements taken from a large series of *Nomia melanderi* larvae in Utah suggest the presence of four larval instars, although in this same paper they do not rule out the possibility of an earlier molt occurring without appreciable change in size. Four larval instars are inferred in the Australian ceratinine genus *Allodapula* (Syed, 1963) and this number is considered to be the rule among most bees. Linsley *et al.* (1952) recorded three larval instars in the bee *Diadasia consociata* Timberlake.

The apparent lack of precise information on developmental stages among bees prompted this ancillary investigation on the development of the alkali bee, *Nomia melanderi*. The observations and experimental data were gathered in the Snake River Valley of eastern Oregon from 1961 to 1964.

METHODS

Cells containing pollen balls with newly laid eggs were collected before 8 a.m. or after 8 p.m. to minimize the temperature and hu-

[1] Technical Paper No. 2104, Oregon Agricultural Experiment Station. Program supported in part by National Science Foundation Grant No. GB-3657.
[2] Present address: Stanislaus State College, Turlock, California.

midity differences between that of the cell contents and the open air. An excavation was made to the cell level using a shovel, following which each cell was carefully probed out with a knife and a small spoon. Each cell containing a pollen ball and an egg was separated from excess soil, taking care to keep the lower one-half to two-thirds of the cell intact and free of cracks. Approximately six such cells were transferred to each seamless tin container half-filled with soil taken from the brood level. The tins were quickly sealed to avoid humidity and temperature changes and taken to a basement room having a temperature of 24 ± 1° C. Upon arrival in the rearing room each cell was carefully examined microscopically and all soil particles were removed from the cell, egg, and pollen ball. Experience has shown that it is in the proximity of the soil particle that fungal growth usually begins. Soil particles were removed by means of a moist probing needle or camel's hair brush. After each of the cells and its contents had been cleaned it was placed in such a position that it could be observed microscopically without further disturbance. A small soil particle was then placed on the dorsum of the anterior end of the egg. As segmentation proceeded, the marker could be observed on the vertex of the head. Once the chorion or exuviae were shed a new marker was placed on the vertex. In this manner it could be determined exactly when the molts had occurred. Fungal growth in the cells was successfully controlled by dipping a camel's hair brush into a solution of 50% propionic acid and gently touching the brush to the affected area. If the mycelia were on the pollen ball, a probing needle was dipped into the propionic acid and then used to gently scrape the fungus off.

Moisture was maintained by keeping the seamless tin containers tightly sealed except when observations were being made. It was usually necessary to add a small amount of moisture to some of the cells by the 5th day. Moisture requirement was most readily determined by observing changes in the fluidity at the feeding site on the pollen ball, and to a lesser degree by noting the condition of the soil surrounding the cell. Moisture was added by gently touching a pipette filled with water to the soil immediately about the cell.

Observations were made and data recorded three times during each 24-hour period.

RESULTS AND DISCUSSION

The data from morning and evening observations on eight specimens are recorded in Table 1. They include the time of eclosion, head

Table 1.—Head capsule diameter in mm of eight *Nomia melanderi* larvae.

Date	Temp °C	Time	1	2	3	4	5	6	7	8
July 30	24°	8 p.m.	E	E	E	–	–	–	–	–
July 31	24°	8 a.m.	E	0.68	E	–	–	–	–	–
July 31	24°	8 p.m.	E	0.82	E	–	–	–	–	–
Aug. 1	24°	8 a.m.	0.68	0.82	0.68	–	–	–	–	–
Aug. 1	24°	8 p.m.	0.68	1.04	0.68	–	–	–	–	–
Aug. 2	24°	8 a.m.	0.82	1.04	0.80	–	–	–	–	E
Aug. 2	24°	8 p.m.	0.82	1.04	0.80	–	–	–	–	E
Aug. 3	24°	8 a.m.	1.04	1.04	0.80	–	–	–	–	0.74
Aug. 3	24°	8 p.m.	1.04	1.25	1.04	E	E	E	E	0.88
Aug. 4	24°	8 a.m.	1.04	1.25	1.04	E	0.72	E	E	0.88
Aug. 4	24°	8 p.m.	1.04	1.25	1.04	E	0.86	E	E	1.05
Aug. 5	24°	8 a.m.	1.20	1.25	1.27	E	0.86	0.72	0.78	1.05
Aug. 5	24°	8 p.m.	1.20	1.25	1.27	E	1.04	0.72	0.78	1.05
Aug. 6	24°	8 a.m.	1.20	1.52	1.27	E	1.04	0.88	0.88	1.29
Aug. 6	24°	8 p.m.	1.20	1.52	1.27	0.70	1.25	1.07	1.04	1.29
Aug. 7	23.5°	8 a.m.	1.20	1.52	1.27	0.80	1.25	1.07	1.04	1.29
Aug. 7	23.5°	8 p.m.	1.48	1.52	1.56	0.80	1.25	1.07	1.27	1.29
Aug. 8	24°	8 a.m.	1.48	1.52	1.56	0.99	1.25	1.27	1.27	1.56
Aug. 8	24°	8 p.m.	1.48	1.52	1.56	0.99	1.25	1.27	1.27	1.56
Aug. 9	25°	8 a.m.	1.48	1.52	1.56	1.20	1.56	1.27	1.27	1.56
Aug. 9	25°	8 p.m.	1.48	1.52	1.56	1.20	1.56	1.27	1.27	1.56
Aug. 10	24°	8 a.m.	1.48	1.52+	1.56+	1.20	1.56	1.56	1.56	1.56
Aug. 10	24°	8 p.m.	1.48	1.52	1.56	1.20	1.56	1.56	1.56	1.56
Aug. 11	24°	8 a.m.	1.48+	1.52	1.56	1.20	1.56	1.56	1.56	1.56
Aug. 11	24°	8 p.m.	1.48	1.52	1.56	1.56	1.56	1.56	1.56	1.56+
Aug. 12	24°	8 a.m.	1.48	1.52	1.56	1.56	1.56	1.56	1.56	1.56
Aug. 12	24°	8 p.m.	1.48	1.52*	1.56	1.56	1.56	1.56+	1.56	1.56
Aug. 13	24°	8 a.m.	1.48	1.52	1.56	1.56	1.56	1.56	1.56+	1.56
Aug. 13	24°	8 p.m.	1.48	1.52	1.56*	1.56	1.56	1.56	1.56	1.56
Aug. 14	24°	8 a.m.	1.48	1.52	1.56	1.56	1.56	1.56	1.56	1.56*
Aug. 14	24°	8 p.m.	1.48	1.52	1.56	1.56	1.56+	1.56	1.56	1.56
Aug. 15	24°	8 a.m.	1.48	PP	1.56	1.56	1.56	1.56	1.56	1.56
Aug. 15	24°	8 p.m.	1.48*		1.56	1.56	1.56	1.56*	1.56	1.56
Aug. 16	23.5°	8 a.m.	1.48		1.56	1.56	1.56	1.56	1.56	1.56
Aug. 16	24°	8 p.m.	1.48		PP	1.56	1.56	1.56	1.56	1.56
Aug. 17	24°	8 a.m.	1.48			1.56	1.56	1.56	1.56	1.56
Aug. 17	24°	8 p.m.	PP			Dead	1.56	PP	1.56*	PP
Aug. 18	24°	8 a.m.					1.56*		1.56	
Aug. 18	24°	8 p.m.					1.56		1.56	
Aug. 19	24°	8 a.m.					1.56		1.56	
Aug. 19	24°	8 p.m.					1.56		PP	
Aug. 20	23°	8 a.m.					1.56			
Aug. 20	23°	8 p.m.					1.56			
Aug. 21	23°	8 a.m.					PP			

+ Pollen consumed. * Defecation began. PP Prepupa.

capsule measurements, the time at which the pollen ball was consumed, the time of initial defecation, and the time at which prepupation occurred. The data clearly show that there are five larval instars in *Nomia melanderi*. Fourteen to 20 days elapsed between oviposition and prepupation. This is in accord with postlarval development and field studies in this species, which indicate that under optimal conditions a single generation will be completed in slightly less than a month (Stephen, 1965).

The late embryo of the alkali bee is found in an inverted position in the egg until shortly before eclosion, at which time it flips over to assume what is considered to be its normal feeding position.

The data indicate that the time from oviposition to eclosion was 2¼ to 3 days. It was undoubtedly somewhat longer, because we could not be certain as to the actual hour of oviposition in the cells exhumed for these tests. The first and second instars are both of very short duration and the difference in head capsule and body size are very slight. Except for the mandibles and much or all of the head capsule, the first-instar larva is entirely covered with the egg chorion. The mandibles can be observed moving back and forth and occasionally both fluid and pollen grains can be detected as they are consumed. Bertholf (1925) reported that in the honey bee the chorion remained in place until a drop of water or larval food was added, whereupon it floated to the surface of the liquid and the larva was freed. He did not consider this as an instar in the honey bee, but there can be no doubt that it is the true first instar in *N. melanderi*.

With the shedding of both the chorion and exuvia of the first instar, the soil particle marker on the vertex was observed to move ventrally and posteriorly. It is noteworthy that the larger head capsule diameters of the first-instar larvae approximate the smaller head capsule measurements of the second instar, so that unless larvae were reared individually it would be difficult and sometimes impossible to distinguish between the two. Differences in head capsule and body size in the third, fourth, and fifth instars were much more pronounced. The third instar lasted from 24 to 48 hours, the fourth for 48 to 60 hours, and the period from the beginning of the fifth instar to the time of prepupation ranged from 7½ to 12 days. It can be noted from Table 1 that the pollen ball is usually consumed in 3 to 5 days after the beginning of the fifth instar and defecation does not begin until 2½ to 4½ days later. This is at odds with an earlier report, based on incomplete data, that defecation began in the species within a day or two following the consumption of the pollen ball (Stephen, 1959).

The entire pollen ball was consumed in 8 to 11 days, a period which corresponds with estimates made in earlier papers.

There is no doubt that the larvae reared under the conditions of the experiment were held at temperatures lower than the daily maxima usually reached under field conditions. The soil temperatures taken at the various beds throughout Oregon at the brood cell level often reach 30° C for short periods during the middle of each day and in California temperatures of 35° C at the brood level are not uncommon. There is no doubt that the development of *N. melanderi* would proceed at a sharply accelerated rate at temperatures above those at which the larvae were held in this experiment. Field observations in Utah and California confirm this conclusion (Bohart and Cross, 1955; Stephen, *in litt.*).

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